

EVOLUTION OF ZOOCECIDIA

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(WITH PLATES XXI, XXII)

The basic conceptions back of the present treatment of the zoocecidial problem are those connoted by the word evolution. For some time the idea that galls have had their phylogeny along with other organisms and parts of organisms has occupied a prominent place in the mind of the writer. Definite attention to this phase of the zoocecidial problem has resulted in the development of outlines of the probable evolution in the various gall groups. This paper is an attempt to give in outline merely the phylogeny of zoocecidia, based in lesser part on embryological data, in greater part on comparative morphological material. Paleontological research has brought so few forms to light that no assistance can be gained from that source. A discussion of the conceptions which are basic for such a treatment of zoocecidia is also given, together with the elucidation of a new interpretation pertaining to the relation of the lower and higher galls.

Historical

In very few papers dealing with the comparative morphological aspects of galls has any attention been devoted to phylogenetic problems; the emphasis has been on the delineation of anatomical detail. No definite studies from a strictly phylogenetic point of view seem to have been made by Europeans. KÜSTER'S recent and extensive studies (9, 10) do not include this point of view, at least not as gall phylogeny is interpreted by the writer.

At the outset careful distinction must be made between conceptions which are basic for the development of phylogenetic outlines and the phylogenetic outlines or "trees" themselves. Historically two interpretations which are basic for the development of zoocecidial phylogenies are extant: (1) gall characters are merely the reappearance of the host plant characters, either those immediately present or those hypothetically latent in the germ

plasm (meristem); (2) gall characters are the result of the influence of both the plant and the animal, chiefly the plant in the lower galls and chiefly the animal in the higher galls. In connection with the first interpretation, KÜSTER (10) expresses his astonishment at the multiplicity of the possibilities possessed by the cells composing the leaves. This consideration of the exceptional normal forms does not enable him to foresee this multiplicity, and throughout his writings there is the same emphasis. The plant cells are loaded with reaction possibilities, due, as KÜSTER intimates, to the retention of an array of latent characters acquired in the course of evolution. His example of the *Adelges* gall on spruce as being similar to the normal cone of *Sciadopitys* is a case in point.

COSENS and SINCLAIR (4), in a study of certain willow galls, present a similar interpretation. They say "The reinstatement in a gall of vestigial characteristics of the plant has an important bearing on the question of gall formation." They recognize, however, "a directive control over the activities of the protoplasm of the host" on the part of the cecidozoon, the result of which is referred to as an "environmental modification." The force of this recognition is weakened by their final statement that "there remains no authentic instance of any organ or tissue in a gall that is new, ontogenetically or phylogenetically, to the host."

With regard to the second interpretation, although a number of European writers, ADLER, FOCKEU, and others, have recognized the essential "independence" of the higher galls (prosoplasmas of KÜSTER), they have not gone so far as to formulate any definite conceptions of gall phylogeny; only the recognition of the fact that certain galls show characters which could not possibly have sprung from the plant has been given.

For the introduction of some genuine phylogenetic theories we must refer to COOK'S (2) study, which gives such statements as the following:

The morphological character of the gall depends upon the genus of the insect producing it rather than upon the plant on which it is produced. The families show parallel lines of development from a low form up to a high form. The Acarin may be considered the lowest group of galls, the Aphidid the next higher, the Cecidomyia galls the next higher, and the Cynipidous galls the highest. However, many of the Cynipidous galls are lower than the Aphidid galls.

Thus COOK, in his recognition of the correlation between the taxonomic position of the gall-making animal groups and the degree of complexity of the galls produced by them respectively, has laid, in part, the foundation for the present discussion. In COOK's papers, however, anatomy and etiology are his major concern. Only in the instance of a few cynipid galls did he present the probable phylogenetic relationships.

Basic data involved in phylogenies

BEYERINCK (1), in his primary division of galls into those characterized by indefinite growth and those exhibiting definite growth, made an initial contribution of great significance. KÜSTER amplified this conception into the following two groups: (1) *Kataplasmata*; all those galls which are characterized by inconstancy and indefiniteness with regard to size and tissue form characters; there is also associated an indefinite time element; they invariably fall below corresponding normal parts in their differentiation, and what differentiation does ensue shows no new fundamental orientation of tissues as contrasted with the normal arrangement; (2) *Prosoplasmas*; all those galls which are characterized by definite size, tissue form, and time of development; in their differentiation they are not so much below the normal as they are different from the normal; in their form characters and orientation of tissues they are fundamentally different from the normal; they may be different in other characters as well, such as quality and quantity of organic substances contained.

KÜSTER (9, 10) has a preliminary division, his so-called "organoides and histoides" groups. Since the first, consisting of very slight modifications of normal organs, can be interpreted as very primitive *kataplasmata*, there is no significance to this classification; in the opinion of the writer it may well be discounted.

Major phylogenetic factors

1. THE PLANT.—The influence of the plant and its evolution are most strikingly observed in the *kataplasmata*, since these structures are for the most part not very far removed in their constitution from the condition obtaining in the normal plant. They

vary from the simplest type in which there is but a slight inhibition of differentiation, to the advanced condition in which differentiation is practically inhibited, only a mass of homogeneous tissue resulting. In the prosoplasmas the contribution of the plant is practically confined to the furnishing of cell types merely, and not differentiation and tissue form conditions.

2. THE ADULT CECIDOZOOON (IMAGO).—(a) *Structural aspects*.—In the lowest cecidozoons, Rotifera, Copepoda, Nematoda, and Acarina, the adult stages as well as the larval stages are concerned in gall-making. With some unimportant exceptions in the Acarina galls, the cecidia are all kataplasmas. Above these groups we have but one genus in which the adult is concerned in definite gall formation, the genus *Pontania* of the Tenthredinidae (saw flies). The terebra's mechanical injury plus the introduction of a specific liquid substance results in a kataplasma of an advanced type, for the lack of differentiated tissues is a striking characteristic of these galls. The prevailing condition among insect cecidozoons, however, is that in which the larval stages only are concerned in gall formation. This is invariably true if the galls are prosoplasmas.

(b) *Behavior aspects*.—Throughout all gall-making groups the instinctive behavior of the adults is a factor with regard to resultant gall conditions. Choice of plant part attacked, number of eggs laid at one point, time of attack, all have something to do with resultant characters. From the standpoint of the fundamental nature and specificity of the individual gall, however, these behavior aspects play but a very minor rôle.

3. THE LARVAL CECIDOZOOON.—In the larval cecidozoon and its evolution we find par excellence the creators of phylogenetic lines, for all prosoplasmas, as heretofore indicated, are the result of larval and not adult activity. Another generalization is the fact that prosoplasmas are practically confined to the Insecta; only a few low prosoplasmas of the Acarina are an exception.

Phylogenies of zoocecidia

Before presenting the outlines of the phylogeny in the various groups it will be desirable to point out some fundamental relationships between the kataplasmas and the prosoplasmas. KÜSTER,

although accurately distinguishing these two groups, curiously enough failed to see any relationship between them from an evolutionary standpoint. Nor has any other writer since this classification has been developed pointed out the very evident situation which exists. That the prosoplasmas in all cases are derived from the kataplasmas is self evident. This fundamental conception, together with an interpretation of it to be given later, forms the central thesis of this paper. On it has been built the diagrammatic presentation of the phylogenetic lines of the higher cecidozoon groups. Following the explanation of these which follows, a more detailed discussion of the general theoretical situation will be presented.

The phylogenetic lines

Attention should be called to the polyphyletic origin of galls, the cecidia-making habit having appeared independently in many diverse groups. Within certain phyla (ex. Nematoda) it appeared among a few closely related genera, while in certain families (ex. Itonididae) it probably had an independent origin in many genera. The "phylogenetic trees" of the various groups (pls. XXI, XXII) are arranged horizontally with some regard to the evolutionary position of the cecidozoon groups. Vertically, the figures are arranged on the basis of their classification into kataplasmas or prosoplasmas. The figures of the galls, while drawn more or less diagrammatically, are based on actual species. They have been chosen to represent fundamental types only. Practically all of them show the galls as seen in section, this being necessary to bring out such salient characters as position of cecidozoon, orientation with regard to plant parts, and the differentiation of sclerenchyma in certain prosoplasmas, this latter being indicated by a dark layer within the body of the gall. The lines or "trees" are based on cecidozoon groups of varying degrees of position in the systematic scale. None below families have been attempted, although an ideal study would present the genus as the unit. At the present time, however, this is not possible through lack of anatomical data. In the discussion of each group some mention will be made relative to the number of genera involved.

ROTIFERA (pl. XXI).—Only one rotifer gall is known. It consists of simple enlargements of the ends of filaments of *Vaucheria* (1) which harbor at their center the cecidozoon. They are to be regarded as extremely simple kataplasmas.

COPEPODA (pl. XXI).—Represented by one form only, a simple kataplasma (1).

NEMATODA (pl. XXI).—Represented by two genera, one using the roots (1), the other the aerial parts (2), producing simple kataplasmas in both instances. The root inhabiting form produces the greatest modification.

ACARINA (pl. XXI).—These galls are chiefly the work of the members of the genus *Eriophyes*. Two fundamental lines of evolution are evident: the production of numerous aborted parts (kataplasmas) from stems, buds, and leaves (1, 2); and a leaf gall line beginning with the erineum (mat of trichomes) stage (3) and passing into the diverticulum condition (5) or the leaf edge-roll state (6). From the leaf blade the erineum-forming type may change its point of attack to the rachis or petiole with more or less hyperplasia and hypertrophy of the hypodermal cells. Such an unusual form is seen in (4). The shallow diverticulum has given origin to the elementary prosoplasma leaf types as represented by (7-10). The figures with their connecting arrows are self-explanatory. It is believed that a type like that shown in (9), which is devoid of trichomes, has been derived from the trichome-bearing kinds. The prosoplasmas of the *Acarina* are of the simplest variety. In the entire absence of sclerenchyma layers and in the non-deviation from the primitive pouch type they constitute as a group the lowest of the prosoplasmas.

ORTHOPTERA (pl. XXI).—Only one genus is represented (1), forming an inconsiderable kataplasma consisting of aborted stem and leaves.

NEUROPTERA (pl. XXI).—A simple cortical swelling constituting a very primitive kataplasma (1) is only reported for this group.

THYSANOPTERA (pl. XXI).—These tropical galls are all of the kataplastic type, the most primitive of which is the simple leaf fold (1), from which the more specialized condition shown in (2) has been derived. A simple curled edge probably represents

another derived type (3), although this may be interpreted as having an independent origin.

COLEOPTERA (pl. XXI).—Despite the vast size of this order and the intimate food relation many of its members hold with living plants, there has been but a slight development of the gall-making habit. They may all be included under the type shown (1), which is a simple cortical kataplasma.

LEPIDOPTERA (pl. XXI).—These are all stem galls of simple constitution. A number of the insect families are involved. The hyperplasia commonly affects all tissues about equally, so that there is merely a local enlargement of the stem (1), with a cavity occupying the pith region. The differentiation is uniformly weaker than in the normal stem; it is a low kataplasma.

The Lepidoptera and the Coleoptera are commonly given a higher position than the Hemiptera which follow. Since they show no complex gall phylogenies, they are placed out of position near a few other unimportant groups.

PSYLLIDAE (Hemiptera) (pl. XXI).—Three original lines of attack on the plant appear to have been made in this group, two of which (1 and 10) end blindly in inconsequential kataplasmas. The third primitive form, simple leaf fold (2), is probably ancestral to the simple leaf edge-roll (9) and a diverticulum kataplasma (3), from which type certain highly specialized prosoplasmas are believed to have sprung. The psyllid prosoplasmas, which are only known from America where they occur on the buds and leaves of the hackberry (*Celtis*), constitute in themselves an excellent evolutionary series, the main outlines of which are indicated in the diagram (4-8). The presence in all of them of specific sclerenchyma layers, together with other highly defined tissue form characters, makes them striking examples of prosoplasmas. No related kataplasmas, that is, on the same host, are now existent.

APHIDIDAE (Hemiptera) (pl. XXI).—All of the galls of this group probably have sprung from the simple leaf fold (1), which, since the insects are commonly numerous locally, appears in the highly variable compound form or the crumpled, wrinkled, or otherwise distorted blade. The number of these primitive aphid leaf convolutions is legion. From these have sprung the indefinite edge-

roll condition (7) and the variable pouch type (2). This latter in turn has given origin to such a kataplasma as shown in (3); which represents the work of many individuals, and the prosoplasma (5), which represents the work of but one insect, the stem mother. From the former has been derived such a spine-bearing prosoplasma as outlined in (4), from the latter the walled forms, the "umwallungen Gallen" of KÜSTER (6), have had their origin. In these no diverticulum structure whatever appears, but the larva is walled in by a vertical upgrowth from the blade. Once this type of gall is attained, the insect is able to use the more rigid parts of the plant, namely, petioles and stems of the season, as a basis for gall formation. None of the aphid prosoplasmas have reached the level at which a sclerenchyma layer is differentiated in them.

COCCIDAE (Hemiptera) (pl. XXI).—Three fundamental primitive kataplasmas can be distinguished in the Coccidae forms, the simple umbo on the stem (1), the shallow leaf pocket (5), and the saucer-shaped incept of the up-walled type. From the latter have arisen those remarkable Australian prosoplasmas characterized by differentiation on the sex basis, that is, the male and female larvae produce differently shaped and constructed galls (4a, male; 4b, female). One of these (3) shows the development of appendages borne on radiating arms. Its form is more primitive than the gall of (4), and in the absence of anatomical data pertaining to any of these forms, it is tentatively given a lower position. I can only find the statement that the female galls are "woody"; the information as to whether or not specific sclerenchyma layers are differentiated has not been obtained.

MUSIDAE (Diptera) (pl. XXII).—Gathered together under this superfamily name are a number of related dipterous families which are represented by kataplasmas only. Three fundamental beginning stages can be distinguished, related to the plant part attacked: a simple rosette resulting from the abortion of the stem axis with concomitant abortion of leaf elements (1), a simple cortical swelling (2), and the hyperplasia of the floral disk in certain Compositae (4). As an advance on the second are those cases in which the larva goes deeper, taking a central position in the stem, giving the intercalate globular type (3).

ITONIDIDAE (Diptera) (pl. XXII).—Numerically this is the largest group of gall producers. Many of the galls attain high evolutionary level, but not as high as many cecidia of the Cynipidae (Hymenoptera), which rivals this group in number and complexity. The most primitive gall of the Itonididae (Cecidomyiidae) is the simple leaf fold, a principal vein constituting the gall axis (1). Conceivably all others may be derived from this, if we grant the possibility of the necessary changes in the insect's instinctive behavior so that other plant parts are persistently attacked and used. Certain of these primitive galls, however, might have appeared independently. Both situations are shown in the diagram.

From the initial leaf fold was evolved the variable ill-defined pocket type (2), which in turn gave rise to the simple prosoplasma of (3). This advances either through the differentiation within it of a sclerenchyma layer (4), or through the partial transfer of the gall toward the upper side of the leaf (5). From this type we have a striking advance through the sclerenchymatized cecidium (6) to the type characterized by a dehiscing larval cell formed by the lignified tissue together with the lining of parenchymatous nutritive tissue. In (8) we have the attainment of the full up-walled ("umwallungen") condition which is believed to have been derived, as indicated, from the diverticulum or pouch form. The majority of up-walled galls show the advanced state, however, through their containing a scleride zone (9). From the up-walled type (8) there has also been derived the interesting double chambered form (11), with the type shown in (10) as an intermediate condition. Excellent examples illustrating all stages of this latter evolution series have been described by the writer (11) from the hickory (*Carya*).

Originating either independently or from the itonid insect which produces the simplest leaf type, we have the burrowing form which causes the "blister" gall (14). A form of this kind attacking the embryonic fruit gives the situation shown in (15), or becoming more specialized on the leaf gives us the prosoplasma (16), or attacking the stem initiates a series of stem galls (17-20), going over into the prosoplasma region with the attainment of

sclerenchyma layers around the larval chambers. If the apical meristem is used as a basis of operation, we get such a primitive gall as shown in (21), and, either through a burying process on the part of the larva or through the up-walling mode of overgrowth, we pass through such a stage as (22) to the prosoplasmatic condition of (23), ending in such a highly specialized type as shown in (24).

CHALCIDAE (Hymenoptera) (pl. XXII).—This family is represented very insignificantly by a few genera producing simple cortical enlargements (1).

TENTHREDINIDAE (Hymenoptera) (pl. XXII).—A few genera of gall makers represent this family. Some species form simple, cortical stem hyperplasias (1); others a rather well defined leaf gall with such homogeneous tissue within it that it may be regarded as but a high kataplasma (2). One European form produces a very low kataplasma in inducing an enrolled condition of the leaf (3). The second form is of especial interest because its initial stages are known to be induced through the action of a chemical stimulus emitted by the adult female at the time of egg-laying.

CYNIPIDAE (Hymenoptera) (pl. XXII).—This family is recognized by all students to be the most remarkable from the standpoint of variety and complexity of the galls produced. This is true even though the largest number of these galls is found on one host genus (*Quercus*). The vast majority of cynipid galls are prosoplasmas. Four independent points of origin are presented, though three of these may conceivably have been derived from the primitive leaf kataplasma (10), as indicated by the arrow lines.

In the evolution of the stem galls we find a progressive series (1-4) related to the orientation of the larva within the stem. This situation is related primarily to the placing of the egg by the ovipositor of the adult females, for so far as known these larvae are not migratory. Any of the stem kataplasmas shown may become elementary prosoplasmas through the differentiation of a sclerenchyma layer around the larval chambers, a parenchymatous nutritive layer being left as a lining. In the diagram only the medullary (4) and cortical (5) types of prosoplasmas are shown. From the latter has been evolved the interesting dehiscence form shown in (6).

The bud and apical meristem galls are shown in (7-9). In (7) a number of the bud leaves merely become fused, while the other two show the transition from the sclerenchymatized polythalamous condition with relatively long, aborted leaves forming an involucre to the sclerenchymatized monothalamous state with shorter, involucre-like elements. In many prosoplasmas of this type the involucre structures are suppressed altogether.

The most primitive cynipid gall is believed to be the variable, generally polythalamous, slightly differentiated kataplasma shown in (10). From this type through the attainment of the "protective" layers the simple prosoplasma (13) is reached, from which by reduction to the monothalamous stage an important stock type (14) is obtained. This latter, however, may also have been evolved through reduction of chamber number before sclerenchymatization had taken place (11). The gall is shown in its primitive intercalate position in the leaf. The prosoplasma variant from the latter is shown in (12).

From the concentrically built stock type (14), which is regarded as an appendicular form, the greatest evolution in prosoplasmas has taken place. Six fundamental lines appear to have sprung from it. Certain characters evolved in and characteristic of these different lines are in special instances combined in the same gall. For example, the stalked type (19) may also exhibit the free larval cell condition of (22), as found in *Dryophanta pedunculata* Bass. The combination, however, of two or more of these fundamental type characters in the same gall is the less common condition; for the most part the galls can be associated with one or the other of the structural evolutionary lines. The same tendency, previously observed in the Itonididae, toward the formation of a distal false chamber, is found (15). This culminates in such a bizarre bracteate form as that shown in (16), a new gall discovered recently by the writer in North Carolina.

Another striking series is that of the evolution of the radiate-fiber type of gall. This begins with the appearance of aeriferous tissue in the cortical region (17), and ends with the condition in which only the fibrovascular bundles traverse the cortical region (18). The type shown in (22) may have been derived from the

latter through the elimination of the bundles, but it may also have had an independent origin from the stock type; embryological evidence in this connection is not available.

The pedicellate condition (19) constitutes the culmination of another line, in which all possible stages may be found in the oak cynipids.

A special place has been given to those galls (20) which bear appendages on the gall body proper (larva containing region). It is believed these bracteate forms for the most part are derived from the non-bracteate forms. There are, however, such possible exceptions as the gall of *Rhodites rosae* L. or *R. bicolor* Harr., in which instances the appendages might be interpreted to be but the reappearance of certain normal parts. In so far as this is true they would be kataplasmic.

In (21) is represented a type possessing highly elongated trichomes. All gradations from the smooth stock type (14) to extreme pubescence are known in the cynipid cecidial biota.

It is better for the present to consider the free larval cell type (22) as an independent line, although, as already indicated, it may have been derived from the radiate-fiber form.

A final line is that leading to the obliteration of the parenchymatous cortical region (23), resulting in a firm, thin-walled structure. These galls are all very small.

Before closing the account of the Cynipidae, mention should be made of the kataplasma shown in (24). Larva cells are organized in the homogeneous tissue of the acorn. This may have arisen independently, or with greater probability it was derived through a change in point of attack on the part of insects forming a primitive leaf gall.

Summary of phylogenetic data

It will be desirable to point out certain major evolutionary tendencies appearing in widely separated groups which point toward an orthogenetic interpretation. (1) The tendency toward specific sclerenchymatization in the formation of the lignified tissue forming the so-called protective layers in the galls. This has appeared independently in Psyllidae, Itonididae, and Cynipidae;

in all of which it is a prominent character in the majority of their prosoplasmas. (2) The tendency toward the up-walled ("umwallungen") condition. This is partially attained in the Acarina and Psyllidae, fully attained in the Aphididae, Coccidae, Itonididae, and is superimposed as the distal false chamber on certain galls of the Itonididae and Cynipidae. (3) The tendency toward the dehiscent type. This is much more restricted, appearing only in the Itonididae and the Cynipidae. (4) The tendency toward appendicular structures borne by the galls. This tendency is almost confined to the Cynipidae. It has appeared in a weak degree in other groups, as in the Aphididae and in certain hickory itonids in which the gall base flares out into ill-defined processes. In the Cynipidae a great variety of appendages is found for which it is not possible to find homologues anywhere on the host plant. Many minor tendencies can be traced out in gall phylogeny studies which may only be mentioned in this general paper. Among such are those toward certain forms, those toward certain orientations of tissues, those toward specializations with regard to certain chemical content (high tannin deposition, etc.), and those associated with the transition from the polythalamous to the monothalamous condition.

Recapitulation data

If zooecidia are amenable to the same evolutionary interpretations as are used in the study of plant and animal parts, then VON BAER'S law should apply to the situation, and this is exactly what is found. Striking examples of recapitulation phenomena may be found in all the larger gall groups, yet, strangely enough, so far as the writer knows, no one has called attention to them or even to the possibility of the law applying in the zooecidial field. The most fundamental fact in this connection is that all prosoplasmas in their ontogeny recapitulate the kataplasma stage. The initial stages of all prosoplasma galls (so far as known), which begin on partially differentiated host tissue, involve a process of dedifferentiation; the tissue is thrown back into a homogeneous condition (full kataplasmic state) out of which grows the new structure. Of course in those instances in which the larva

is from the beginning in contact with meristem, no such regression is possible or necessary. This situation will be developed at greater length in the general discussion.

Within the prosoplasmas themselves innumerable examples of recapitulation may be pointed out, two of which may be mentioned. In the ontogeny of the cecidium *Amphibolips inanis*, the gall passes through the spongy stage illustrated by *Amphibolips confluentus* before it reaches the mature condition with radiating fibers. In the ontogeny of *Oligotrophus annulipes* (European) a juvenile stage is passed through which is almost exactly reproduced in an adult gall (*Cecidomyia* sp.) on the same host. HOUARD (7), in reporting the resemblance of these two stages, fails to suggest the evident recapitulation interpretation.

Discussion

The foregoing part of this paper presents the results gained in the application of certain fundamental conceptions regarding cecidia which are concerned with the evolution of these structures. These conceptions have their historical background, as already indicated, but it will be well to review them in the light of modern genetic and phylogenetic theories, and point out their synthesis which, with the application of them in constructing the phylogenetic trees, constitutes the chief contribution of the present paper.

Before entering upon this constructive work, however, it will be necessary to clear the ground of certain false conceptions which have held sway to the present time, such as the interpretation of KÜSTER, COSENS, and others, who hold that all gall characters are but the expression of active or latent normal host plant characters. COSENS and SINCLAIR (4) state that there remains no authentic instance of any organ or tissue in a gall that is new, ontogenetically or phylogenetically. This interpretation is clearly fallacious, for it is the essential newness of prosoplasmas which constitutes their most important characteristic. This newness appears perhaps in its most striking manner in the form characters of the tissues, which implies of course the form of the gall as a whole. Since form characters are of utmost importance

throughout all taxonomic, genetic, and evolutionary studies, certainly these characters must be taken into account by the cecidologist. When the counterparts of these characters cannot be found associated with any normal tissue mass of any plant, they must be regarded as new and not as having had their origin from the plant side. As pointed out by the writer in a previous paper (12), "in prosoplasmas the types of cells found are closely comparable to those of normal plant parts, but the tissue forms (in prosoplasmas) are fundamentally new." KÜSTER (10) speaks very properly of "Die prosoplasmatische Neubildungen," recognizing the fundamentally independent character of the higher galls, but like COSENS fails to recognize that the origin in evolution of the prosoplasmas lies elsewhere than in the constitution of the plant or of the plant's ancestors.

COOK (2) arrived at a proper basis for advance when he saw that "the morphological character of the gall depends upon the genus of insect producing it, rather than upon the plant on which it is produced." COOK, however, failed to use BEYERINCK'S (1) early division of galls into the "indefinite" and "definite" groups (a fundamental situation which KÜSTER later developed), so that his work fell short of a full analysis; for, as has been indicated, the phylogenetic origin of the prosoplasmas from the kataplasmas (within cecidozoon groups) is all important.

This leads to the nucleus of the present interpretation, which holds that in the contemplation of zooecidia two fundamental groups must be recognized, kataplasmas and prosoplasmas, and that there exists a phylogenetic relation between them. The most interesting and significant situation in this connection is that, whether viewed ontogenetically or phylogenetically, kataplasmic development progresses, through a process of increasing inhibition of host characters, from the normal host differentiation to complete homogeneity, upon the attainment of which prosoplasmic development may commence the construction of new differentiations and new forms. The embryological and comparative morphological evidence for this interpretation is overwhelming, as has been indicated in the foregoing accounts of phylogenies and of recapitulation phenomena.

It would appear then, in zoocecidial ontogeny or zoocecidial evolution, that there occurs at first an overcoming or breaking down of the differentiation and morphogenetic mechanisms which bring about the normal expression of the host plant characters. When this has gone on to the point where no differentiation whatever ensues, the new advance is made in the direction of the prosoplasmas in which fundamentally new characters are caused to appear. Thus we have a remarkable turning point in gall evolution, namely, that at which the normal expression of the plant's potentialities, locked up in its meristem, is inhibited. All gall forms, from the most insignificant interference with normal differentiation to total suppression, are kataplasmas, and all those types arising as definite new structures from the final kataplastic condition are prosoplasmas.

As pointed out in connection with the recapitulation data, all prosoplasmas in their ontogeny pass through the kataplastic stage, either in the actual reversion of partially differentiated tissue to the undifferentiated condition; or, if the cecidozoon is in contact with the meristem, there occurs the equivalent, namely, the complete suppression of the plant's tissue characters, only the new ones of the prosoplasma appearing.

For the sake of clarity the situation has been presented in positive, mutually exclusive terms. There exists, as would be expected, a small minority of galls which occupy the transition region between the kataplasmas and the prosoplasmas. In certain of these, for example, prosoplastic characters may exist along with kataplastic ones. Such a gall is that of *Phytophaga rigidae* O.S. discussed by COSENS and SINCLAIR (4), in which aeriferous tissue is found which they explain on the latent character hypothesis. According to this view the gall is kataplastic, but if we take into consideration the specialized structure, the "beak," of the distal end of the gall (an "umwallungen" development), the form character of the scleridal and nutritive tissues (counterparts of which are not to be found in any normal part of the host or its relatives), we must conclude that this gall is also definitely prosoplastic in nature. Thus in many forms both types of tissue characters may appear. It will be questioned at

once in the evolution or ontogeny of zooecidia, how is such a retrogression followed by a progression in a new direction possible? What is the mechanism involved? The effort of all students in attacking this so-called stimulus problem has signally failed to elucidate the situation. In the opinion of the writer this is because the problem goes much deeper than our present technique is able to penetrate, for it is to be classed with the general unsolved problems of growth (ontogeny) and evolution (phylogeny). Just as a mass of cells in an apical growing point, in some unknown manner, certainly has much to do with the differentiation products of that stem, so has the mass of embryonic cells constituting the prosoplasma-making larva much to do with the differentiation products, not only of itself but of the plant tissue around it. It has extended its control (mechanistically interpreted) in the field of form characters (and others to a less degree) beyond the borders of its own body. As FOCKEU (6) has put it: "La feuille est en rapport avec les phenomenes vitaux de la larve" rather than with the normal leaf itself (we would append to bring out the contrast). In other words, we would hold that the development of prosoplasmas is brought about through the superposition of embryonic animal tissue (the cecidozoon larva) on that of embryonic plant tissue with a relation in growth which is an essentially normal one, that is, the mechanism of morphogenesis is operative, but the primary control is with the larva.

This leads to a final statement, one given earlier by the writer (12), to the effect that "the germ plasm of the cecidozoon is the place of origin of gall forms." This, of course, merely falls in with the current general ideas concerning the significance of the germ plasm in evolution. In the germ plasm of the animal originated the factorial conditions which, phylogenetically considered, first gave the embryonic cecidozoon the ability to break up the normal operation of the plant's factors making possible normal plant differentiation, and secondly the factors which initiate the development of new form and other characters expressed in the plant cell masses.

Zooecidial evolution then is a complex in which, in its early stages (kataplasmas) with regard to certain characters, the plant's

germ plasm dominates, while in its later stages (prosoplasmas) the animal's germ plasm gains control; the whole, however, constituting a single progressive series of factorial transformation as far as the changes in the animal germ plasm are concerned.

Summary

1. KÜSTER'S groups, kataplasmas (lower galls of indefinite nature, differentiation conditions similar to, but in complexity below that of normal plant) and prosoplasmas (higher galls of definite nature, differentiation conditions new) are basic for the present paper.

2. Evolutionary concepts are introduced in pointing out that prosoplasmas have arisen from kataplasmas. The probable main outlines (phylogenetic trees) of the natural cecidozoon gall groups are presented for the first time.

3. Kataplastic evolution is held to be a process of progressive inhibition of differentiation ending with tissue homogeneity. Prosoplastic evolution may only begin when homogeneity has been attained, and consists in the development of new form and tissue orientation characters chiefly. In prosoplasma formation, whether viewed ontogenetically or phylogenetically, the insect larva has gained control of the differentiation and morphogenetic mechanisms, so that animal factors come to expression in plant tissue.

4. Origin of significant characters of prosoplasmas lies in change in factorial situation in animal's germ plasm.

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EXPLANATION OF PLATES XXI, XXII

Plate XXI

Rotifera: (1) *Notammata Werneckii* Ehrenb. on *Vaucheria*.

Copepoda: (1) *Harpacticus chelifer* Müller on *Rhodomenia*.

Nematoda: (1) *Heterodera radicicola* Greef on *Lycopersicum*; (2) *Tylenchus devastatrix* Kühn on *Trifolium*.

Acarina: (1) *Eriophyes* sp. on *Fraxinus*; (2) *Eriophyes populi* Nal. on *Populus*; (3) *Eriophyes* sp. on *Fagus*; (4) *Eriophyes* sp. (*anomalum* Cook) on *Juglans*; (5) *Eriophyes* sp. (*querci* Garman) on *Quercus*; (6) *Eriophyes goniothorax* Nal. on *Crataegus*; (7) *Eriophyes* sp. on *Cephalanthus*; (8) *Eriophyes* sp. (*abnormis* Garman) on *Tilia*; (9) *Eriophyes* sp. on *Salix*; (10) *Eriophyes* sp. on *Acer*.

Orthoptera: (1) *Meconema varium* Fabr. on *Quercus*.

Neuroptera: (1) *Lestes viridis* Van der Lind on *Fagus*.

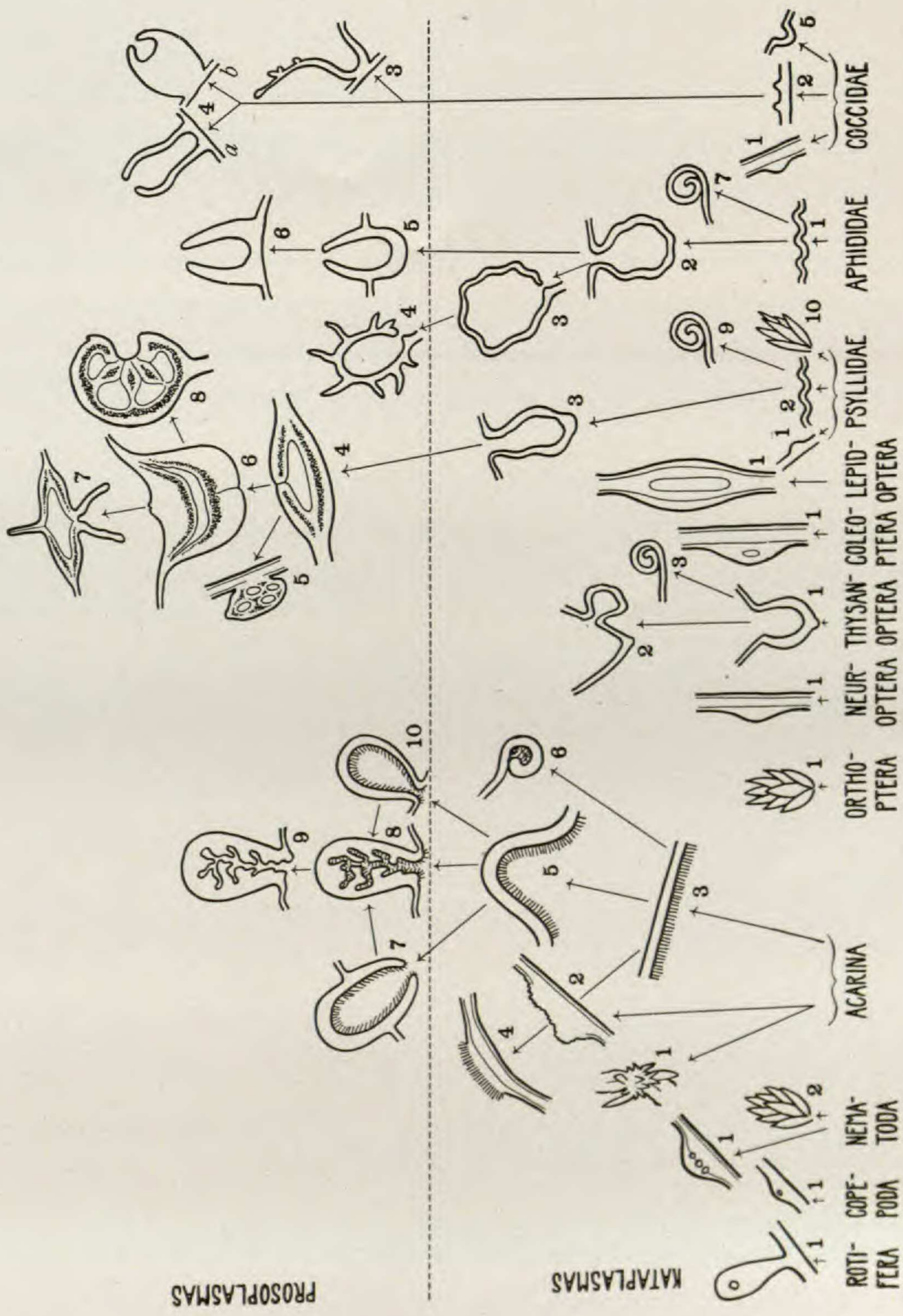
Thysanoptera: (1) *Thrips* sp. on *Piper*; (2) *Thrips* sp. (host not given); (3) *Mesothrips melastomae* Zimm. on *Melastoma*.

Coleoptera: (1) *Mecas inornata* Say on *Populus*.

Lepidoptera: (1) *Gnorimoschema gallaesolidaginis* Riley on *Solidago*.

Psyllidae: (1) *Psylla crataegi* Schrank on *Crataegus*; (2) *Psylla ledi* Flor. on *Ledum*; (3) *Trioza Kiefferi* Giard on *Rhamnus*; (4) *Pachypsylla vesiculum* Riley on *Celtis*; (5) *Pachypsylla gemma* Riley on *Celtis*; (6) *Pachypsylla mamma* Riley on *Celtis*; (7) *Pachypsylla asteriscus* Riley on *Celtis*; (8) *Pachypsylla venusta* Riley on *Celtis*; (9) *Trichopsylla Walkeri* Forster on *Rhamnus*; (10) *Livia maculipennis* Fitch on *Juncus*.

Aphididae: (1) *Myzus ribis* L. on *Ribes*; (2) *Pachypappa marsupialis* Koch on *Populus*; (3) *Pemphigus vagabundus* Walsh on *Populus*; (4) *Hamamelistes spinosus* Shimer on *Hamamelis*; (5) *Phylloxera conica* Shimer on *Carya*; (6) *Phylloxera caryaecaulis* Fitch on *Carya*; (7) *Chaitophorus leucomelas* Koch on *Populus*.



PROSOPPLASMAS

KATAPLASMAS

ROTI-FERA
COPE-PODA

NEMA-TODA

ACARINA

ORTHOPTERA

NEUROPTERA
THYSANOPTERA
COLEOPTERA
LEPIDOPTERA

PSYLLIDAE

APHIDIDAE

COCCIDAE

WELLS on ZOOCECIDIA